B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 27 MAY 1977 NUMBER 442

A LABORATORY STUDY OF THE TURKISH HAMSTER *MESOCRICETUS BRANDTI*

CHARLES P. LYMAN[1] AND REGINA C. O'BRIEN[1]

ABSTRACT. Ten years of laboratory observations of a breeding colony of *Mesocricetus* from central Turkey are summarized. From morphological and karyological evidence, as well as cross-breeding experiments, it is concluded that *Mesocricetus brandti* is distributed in specific areas throughout Asiatic Turkey, south into Palestine, Syria, the northern part of Iraq, northwest Iran, and over the Caucasus into Daghestan. The chromosomal polymorphism noted in this species may be due to the isolation of groups to these specific types of terrain.

The reproductive cycle, growth, and care and behavior in the laboratory are described. Records of hibernation are detailed and compared with those of *Mesocricetus auratus*. It is emphasized that *M. brandti* offers a unique opportunity to study the factors which influence hibernation using matched animals of known age and lineage.

INTRODUCTION

The study of hibernation in mammals has long been hampered by the lack of an animal which could be bred and raised readily under laboratory conditions. Ground squirrels, marmots, dormice, European hamsters, hedgehogs and microchiropteran bats have been used extensively as experimental animals, but all of these species are usually obtained by collecting them in the wild.

The Syrian hamster is easily raised in the laboratory and has been used as an experimental animal for more than forty years. However, hibernation in this species is extremely unpredictable, and many individuals fail to hibernate even when exposed to cold for many months (Lyman, 1948, 1954).

[1]Department of Anatomy, Harvard Medical School
Boston, Massachusetts, 02115 and
Museum of Comparative Zoology
Harvard University, Cambridge
Massachusetts 02138

In August, 1965, we obtained 13 hamsters trapped in central Turkey.[1] These animals hibernated readily when exposed to cold (5 ± 2°C) the following winter and bred in the laboratory during the next spring. Since that time, the colony has been continued, detailed notes have been maintained, and various experiments have been undertaken. In 1971, we received an additional 29 animals. We maintained and bred these animals separately from the original group for comparative data.

The two groups resembled each other closely, and clearly differed from laboratory specimens of the Syrian or golden hamster, *Mesocricetus auratus*. As information concerning the Turkish hamsters accumulated, it became apparent that this species is the best experimental animal for the study of certain aspects of hibernation, particularly those which require animals of known history and lineage. Offspring of the two original colonies have been distributed to several investigators and we hope that the Turkish hamster is now established as an experimental animal. For this reason, our knowledge concerning this hamster is detailed below.

Identification is, of course, of critical importance in animals used for experimental studies. However, because of the limited amount of comparative material available, comparisons of skins and skulls have led to conflicting opinions on the taxonomy of *Mesocricetus* (Ognev and Heptner, 1927; Aharoni, 1932; Ellerman, 1941, 1948; Vinogradov and Argiropulo, 1941; Ellerman and Morrison-Scott, 1951; Vereshchagin, 1959; Hamar and Schutowa, 1966; Ivanov, 1969; Raicu et al., 1969; Vorontsov and Krjukova, 1969; Todd et al., 1972). The genus exhibits chromosomal polymorphism while showing relatively few morphological differences over a wide geographic area. Emphasis by some investigators on the analysis of karyotypes has led to divergent taxonomic views which can not be fully reconciled until more definitive data such as chromosomal banding studies and cross-breeding experiments in the laboratory have accumulated. For this reason we have limited ourselves to a consideration of the identity of the Turkish animals and have attempted to delineate their distribution in their natural habitat.

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[1]We are grateful to Dr. Bahtiye Mursaloğlu of the University of Ankara, Ankara, Turkey for making arrangements to obtain the hamsters, and to Mr. Haluk Anat of the same university for trapping the hamsters and supplying us with information concerning their natural history.

TAXONOMIC MATERIALS

The animals which formed our original colony in 1965 were captured by Mr. Haluk Anat in Malya, near Kirsehir (39°N, 34°E)[2] about 125 kilometers (km) southeast of Ankara, Turkey (Fig. 1). Mr. Anat trapped the second group six years later near the city of Ankara. We refer to these two groups collectively as "Turkish" hamsters in this text.

Skins and skulls of hamsters from Malya which had been trapped alive and kept in captivity for varying periods of time were used for comparison with the specimens of *Mesocricetus* in the British Museum.[3] As far as we have been able to determine, the British Museum collection is the only representative collection of this genus in the United Kingdom or the United States. It contains specimens from a now defunct colony in the Wistar Institute which were obtained from Pirbadan [m] (35°N, 48°E), Iranian Kurdistan, a small village 125 km north-northwest of Hamadan, Iran (Fig. 1). Hamsters from this colony have been the subject of karyological and breeding studies and have been referred to as "Kurdistan" or "K" hamsters[4] (Lehman and Macpherson, 1967; Palm, Silvers and Billingham, 1967; Todd et al., 1972; Raicu et al., 1972).

We observed four hamsters originating from a colony of Rumanian hamsters maintained by Dr. Petre Raicu, University of Budapest[5], alive in our laboratory. We used two skins and skulls from the Rumanian colony to compare with the specimens in the British Museum. In addition, hamsters trapped for Dr. Michael Murphy[6] in Aleppo, Syria were maintained in our laboratory for comparative studies and breeding experiments.

Breeding crosses were usually attempted by placing the female in the cage of the male, though occasionally the reverse process was used. In many instances we used vaginal smears to determine the estrous cycle, and exposed the female to the male in the afternoon

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[2]The report that these animals came from Aksehir, Turkey (Todd et al., 1972) is an error derived from faulty original information.

[3]We thank Drs. J. E. Hill and G. B. Corbet of the British Museum for making these specimens available

[4]All place names in this paper are those given in the original articles.

[5]We are grateful to Dr. William Nixon of Randolph, Mass. for supplying these animals.

[6]Dr. Murphy made a trip to Aleppo to obtain this colony and observe their behavior. We acknowledge his gift with thanks.

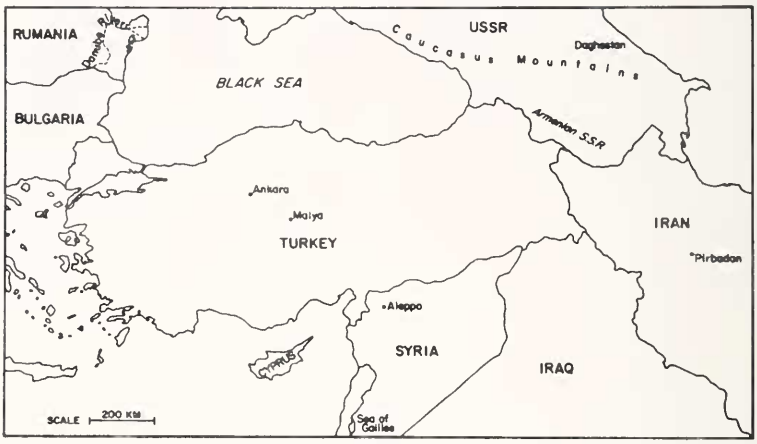

Figure 1. Map showing distribution of *Mesocricetus*.

prior to estrus. If the animals fought, they were separated temporarily, and pairing was attempted at later dates. Otherwise, the animals were left together for three or four days and then separated. The animals were observed for copulatory behavior and vaginal smears were often made if copulation was suspected but not observed.

We prepared karyotypes from metaphase spreads obtained from normally dividing primary skin cultures. The cells were harvested on the seventh to ninth day of culture. After exposure to colchicine (final dilution 36 micrograms per milliliter of medium) for five hours, and hypotonic solution for 10–15 minutes, cells were fixed in 3:1 methanol:glacial acetic acid and stained with Wright-Giemsa stain.

Chromosomes were counted in at least 100 cells per animal. Selected metaphase spreads were photographed and homologous chromosomes were paired in the conventional manner according to their length and position of the centromere.

DISCUSSION OF TAXONOMY

It is generally agreed that the distribution of the genus *Mesocricetus* includes the eastern parts of Rumania and Bulgaria, across Anatolian Turkey into the Caucasus, and south into Syria, the northern tip of Iraq and the northwest part of Iran.

Hamar and Schutowa (1966) have presented the most complete taxonomic investigation of the genus in recent time. They had

available for comparison 102 specimens from the Moscow and Leningrad Zoology Museums as well as the Humbolt Museum in Berlin. Based on morphological data, they recognized three species of one group. They proposed that *Mesocricetus newtoni* was found in eastern Rumania and Bulgaria and that *Mesocricetus auratus* was confined to the type locality of Aleppo, Syria. *Mesocricetus brandti* appeared to occupy the rest of the range of *Mesocricetus* except for an area north of the Caucasus which was occupied by *Mesocricetus raddei* and *M. r. nigriculus.*

Based on cranial measurements, they found little difference between *newtoni, auratus* and *brandti,* but the two forms of *raddei* were distinctly different, with relatively massive skulls and larger molar teeth. The bodies of animals of the *raddei* group were also larger in size, and the black color of their bellies contrasted with the grey or white of the smaller *newtoni-auratus-brandti* group.

Our examination of specimens of *raddei* from the Caucasus in the British Museum and the Museum of Comparative Zoology confirmed the observations of Hamar and Schutowa (1966). These authors summarized their findings by suggesting that *raddei* should be separated from the other group at the subgeneric level, and the evidence presented for this view is convincing.

When compared to specimens from Rumania or Turkey, the dorsal pelage of the Syrian or golden hamster is notably different. The color of the latter is a rich Sanford's brown (Ridgway, 1912) while our animals from Turkey are tawny-olive to Saccardo's umber dorsally, with an overlay of black-tipped guard and pile hair which darkens the pelage. Although Hamar and Schutowa do not emphasize this, our animals from Rumania were darker dorsally than our animals from central Turkey, as were several of the seven Rumanian specimens in the British Museum. The subauricular stripe in the Syrian animals is poorly defined, being a mixture of brown and black hairs, while in the Turkish and Rumanian animals it is pure black. There is a difference in the coloring of the chest, for in the Syrian hamster it is brownish with a narrow white mid-stripe, while in the Turkish and Rumanian animals there is a pronounced bar of black, as illustrated by Hamar and Schutowa (1966). The Kurdistan or "K" specimens were paler on the dorsal surface but otherwise closely resembled our animals, which were trapped approximately 1350 km to the west-northwest.

It is of incidental interest that the pelage of the type specimen of *M. auratus* in the British Museum is indistinguishable from speci-

mens which Dr. Murphy collected in Syria in 1971 and these in turn match the common laboratory Syrian hamster. Thus, laboratory breeding since 1930, when the first animals were captured (Adler, 1948), has not altered the natural coat color of this animal, though many mutations in coat color have occurred.

More than one thousand Turkish hamsters have been raised in our laboratory, and slight differences in the pelage have been observed. Some individuals have darker dorsal pelage than others, and the ventral surface may vary from grey-white to grey, particularly on the abdomen. There are no consistent differences in color between the colony which originated from Malya and the colony from Ankara.

The four living animals from Rumania were about the same size as laboratory strains of Syrian hamsters, but our Turkish hamsters were bigger as full-grown adults. Twenty-one two-year-old Turkish hamsters chosen at random averaged 163 grams (g) with a range of 137 to 258 g. In comparison, 111 two-year-old Syrian hamsters averaged 105 g with a range of 97 to 113 g (Altman and Dittmer, 1964). The heads of the living animals from Rumania differed from the others, for the face was more pointed and ratlike, though the nasal portion of the skulls of Rumanian animals is not narrower.

Laboratory interbreeding experiments have been detailed by Todd et al. (1972) and can be briefly summarized. No offspring have resulted from matings between our animals from Malya or Ankara in Turkey and laboratory animals originating in Syria (Todd et al., 1972; present study), though copulation has been observed (Murphy, personal communication; present study). Attempts to cross Kurdistan animals with laboratory Syrian hamsters have been similarly unsuccessful (Palm et al., 1967).

The cross between Rumanian female and Malya male hamsters has produced viable offspring, but the reciprocal cross has not been attempted. Todd et al. (1972) report the survival of five females, with a male living only two weeks. In our laboratory, a female killed her first litter and two females survived in the second litter, both of which had developed diabetes mellitus by the age of nine weeks. Diabetes was not the invariable result of this cross, however, for we tested a female raised by Todd et al. and found the urine negative for glucose. The hybrids were larger than either parent, with one weighing 293 g as an adult. Todd et al. report copulation between a hybrid Rumanian-Turkish female and a Malya male, but presented no evidence that the hybrid was fertile.

Viable hybrids have been produced in the cross between female hamsters from Kurdistan and males from Rumania, but the reciprocal cross was unsuccessful (Raicu et al., 1972). (Dr. M. Bahmanyar of the Pasteur Institute of Iran collected both Dr. Raicu's and the Wistar Institute hamsters. He writes that the former animals were trapped 25 km west of Pirbadan.) The number of young per litter was small and averaged about 50 per cent of the number expected in non-hybrid litters. Histological examination revealed that both the male and female reproductive organs of the adult hybrids were atrophic, and on this basis both sexes were considered to be totally sterile.

Raicu and Bratosin (1968) and Raicu et al. (1969) have obtained reciprocal crosses between Syrian and Rumanian hamsters. Though the litters were small, the individual animals were large and the gonads of the hybrids appeared histologically atrophic, leading to the conclusion that the animals were sterile. Todd et al. (1972) found that the hybrid females resulting from crosses between Rumanian males and Syrian females would mate with Syrian males. No viable young were produced, though reabsorbing embryos were found at autopsy in three cases.

In contrast, there was no indication of lack of fertility between the two groups of animals from Turkey. Reciprocal crosses in our laboratory between hamsters originating in the Ankara and Malya areas result in normal healthy litters and the F_1 generations are fertile, producing normal young.

The karyotypes of the various groups of hamsters, including hamsters in our laboratory which originated in Malya, have been reported by Todd et al. (1972). Since that time we have established the karyotype of hamsters from the area of Ankara. The latter animals have a diploid number (2N) of 44 chromosomes with a fundamental number of autosomal arms (FN) of 80 (Fig. 2), while in the hamsters from Malya 2N = 42 and FN = 78 (Fig. 3). Hybrids of both sexes were examined and in these 2N = 43 and FN = 79.

In the animals from Ankara, the autosomal complement is composed of two pairs of metacentric chromosomes (#3 and #13), two pairs of acrocentric chromosomes (#19 and #21) and the remaining 16 pairs, which are a graduated series of submetacentric and subtelocentric chromosomes. Because of the similarity and gradation in size of the majority of the chromosomes, it was not possible to identify with complete certainty many individual chromosomes, including X and Y.

Figure 2. Representative karyotype of *Mesocricetus brandti* from the area of Ankara, Turkey. Autosomes are arranged sequentially from upper left to lower right.

In comparing the karyotype of the Ankara hamsters with that of the Malya group the same difficulty obtained, yet it is obvious that the difference in diploid number between the two groups is the result of the absence of the acrocentric pair #19 in the Malya hamsters leaving only one pair of acrocentric chromosomes. The hybrid animals have three acrocentric chromosomes, two small ones and one slightly larger. The X chromosome of the Malya hamster is unmistakably larger than that of the hamster from Ankara.

Comparison of the karyotype of the Ankara hamster with that of the Kurdistan hamster (Lehman and Macpherson, 1967) reveals certain differences. In the Kurdistan hamster 2N = 42 and FN = 80. The smallest autosomal pair appears similar to #20 in the Ankara karyotype and there are no acrocentric elements. The Y chromo-

Figure 3. Representative karyotype of *Mesocricetus brandti* from Malya, Turkey. Autosomes are arranged sequentially from upper left to lower right.

some of the Kurdistan hamster is obviously much larger than that of the Ankara animals.

From the evidence which has accumulated to date, a few conclusions can be drawn. It is apparent that the hamsters of the genus *Mesocricetus* from Anatolia to at least as far east as Iran are not subspecies of the Syrian hamster, *Mesocricetus auratus*, as some authors have suggested (Ellerman and Morrison-Scott, 1951; Vereshchagin, 1959). While wild-caught Syrian, Turkish, or Rumanian hamsters breed readily in captivity with animals from the same area, all attempts to cross the Syrian with the Turkish or Kurdistan hamster have failed. If the animals will not breed in the laboratory under a wide series of conditions, it is unlikely that they would breed in the field. The bright golden brown color of the back,

the absence of black subauricular and chest patches and the creamy white belly plus the smaller size of the Syrian hamster reinforce the concept that *M. auratus* is a separate species.

When Syrian and Rumanian hamsters are compared, the difference in pelage is equally striking. These animals are similar in size, but the Rumanian animals are much darker dorsally and on the belly, have darker chest patches, and the ratlike face is obvious in the live animals. Although viable crosses have been produced in the laboratory, both histological data and attempts at breeding indicate that the F_1 generation is sterile. On the basis of karyological studies (Raicu and Bratosin, 1968) as well as electrophoretic and chromatographic analysis of the blood serum, Raicu et al. (1968, 1969) stated that the Rumanian hamster, *Mesocricetus newtoni,* was a different species from the Syrian hamster, *Mesocricetus auratus,* and the data given above reinforce this conclusion.

The Rumanian hamster is smaller and darker than the Turkish and Kurdistan animals, and the facial appearance in the live Rumanian animals is distinctive, but these differences are not sufficient for specific separation. Crosses between Rumanian hamsters and animals from Malya in central Turkey or from Kurdistan produce viable young, but the F_1 generation is sterile. Furthermore, the occurrence of diabetes in the Rumanian-Turkish cross, and the small litters and failure of reciprocal crossing in the Rumanian-Kurdistan matings, are evidence that the crosses encounter biological barriers sufficient to separate them as species.

When Lehman and Macpherson (1967) described the karyotype of their hamsters from Kurdistan, the animals were tentatively identified by the British Museum as *Mesocricetus brandti* from skins and skulls. Our subsequent comparison with skins and skulls of hamsters from Malya reveal that the two groups resemble each other closely, though the Kurdistan animals are lighter on the dorsal surface. Color photographs of these animals alive, lent through the kindness of Dr. R. E. Billingham of the Wistar Institute, indicate that the animals do not possess the ratlike face which seems to be typical of hamsters from Rumania. After karyotypic examination of hamsters from Kurdistan, Malya, Rumania and Syria, Todd et al. (1972) concluded that the karyotypes of animals from Kurdistan and Malya most closely resembled one another.

The evidence is persuasive that the animals from Malya and Ankara and the Kurdistan hamsters are all *Mesocricetus brandti.* The lighter dorsal pelage of the Kurdistan animals, when compared

to the two colonies from central Turkey and the specimens in the British Museum, suggest that the Kurdistan animals may be a subspecies of *M. brandti*. In this regard, it is of interest that Mr. Anat, who is a trained field naturalist, has written us that the animals in the northeast area of Turkey near Kars are larger and darker than hamsters from central Turkey. Several subspecies of *M. brandti* may exist in Turkey, Armenia and northwest Iran, separated by various geographic barriers.

We conclude that there are three distinct species of small hamsters of the genus *Mesocricetus* in areas south and west of the Caucasus. *Mesocricetus newtoni* inhabits the Dobruja area in the eastern part of Rumania and Bulgaria and, according to Hamar and Schutowa (1966), probably is not found west of the Danube in Rumania. *Mesocricetus brandti* ranges across Anatolian Turkey into the northern part of Iraq and the northwestern portion of Iran. Hamar and Schutowa (1966) and Aharoni (1932) report that *M. brandti* is found south of Aleppo and Aharoni indicates the southern limit is at the latitude of the Sea of Galilee. In contrast to this wide distribution, *M. auratus* appears to be restricted to the area of the type locality of Aleppo, Syria.

For definitive information on the distribution of *Mesocricetus* in and north of the Caucasus, one must turn to investigators who had access to live specimens or collections in Russia. Although there are differences of opinion on the number of subspecies involved, Ognev and Heptner (1927), Vinogradov and Argiropulo (1941), Hamar and Schutowa (1966) and Gromov et al. (1963) all agree that the genus in this area is clearly separable into two species, referred to here as *M. brandti* and M. *raddei*. *M. brandti* are smaller than *M. raddei* and there is no black on their bellies. In their karyological studies, Vorontsov and Krjukova (1969) and Ivanov (1969) also concluded that *M. brandti* and *M. raddei* were specifically different. The *M. brandti* studied by Ivanov came from the Daghestan area and Gromov et al. (1963) state that this species is found in the plains and foothills of Daghestan. Gromov et al. (1963) and several other Russian investigators remark on the discontinuity of the distribution of *M. brandti* in the Caucasus, and we find nothing in the literature to indicate that it is actually sympatric with *M. raddei* in any area.

Todd et al. (1972) reviewed the reported karyotypes of *M. brandti* from Daghestan, Armenia, Iranian Azerbajzan and Erevan, and of a specimen which was probably from Iran. They presented a haploid idiogram comparing the karyotypes of the Kurdistan animals with

our hamsters from Malya, *M. newtoni* from Rumania and laboratory *M. auratus*. The diploid number (2N) of *M. newtoni* was 38, that of *M. auratus* was 44, and that of the various specimens of *M. brandti* was 42. They concluded that the differences in the karyotypes of the samples of *M. brandti*, including the fundamental numbers, was sufficient to suggest that the designation *M. brandti* was being applied to a group of "cryptic" species. At the time their data was collected, it was not known that the karyotypes of hamsters from Malya and Ankara differed both in diploid and in fundamental numbers, though the animals appeared phenotypically similar and produced fertile crosses in the laboratory. Zimmerman (1970) emphasizes the frailty of karyological data when used by itself to determine taxonomic relationships and the breeding success between the Malya and Ankara group reinforces this concept.

Recent evidence indicates that some rodents may be genetically isolated though phenotypically similar. *Spalax* (Nevo and Shkolnik, 1974), *Perognathus* (Patton, 1972), *Thomomys* (Patton, 1973) and *Peromyscus* (Schmidly and Schroeter, 1974) are some of the rodents which have marked chromosomal differences in groups from restricted, contiguous areas. Patton and Dingman (1970) point out that the diversity in karyology often occurs in burrowing rodents with limited dispersibility and small breeding populations. Field reports, particularly those of Argiropulo (1939), and our observations of "field" conditions in the laboratory indicate that hamsters are fossorial rodents, though their way of life is not comparable to that of an animal such as *Thomomys*, which spends virtually its whole existence underground. Aharoni (1932) and Argiropulo (1939) both emphasize that *Mesocricetus* is found in very specific types of habitat and Argiropulo states that the distribution of *brandti* in Armenia is limited to specific altitudes. Mr. Anat has written us that there was no available open water in the areas where he trapped our animals, yet we find that hamsters in the laboratory which are fed laboratory rat chow cannot survive without water to drink. Thus, *brandti* in some areas must depend on metabolic water and water in their food, and this must limit their distribution. Furthermore, Argiropulo states that they never live in wooded areas. These factors, coupled with their slow locomotion, may limit *brandti* to very specific types of habitat and isolate one group from another, which may explain why the karyotype of each population of this species examined to date differs from the other.

Aharoni (1932) points out that the Syrian hamster is confined to the immediate vicinity of Aleppo and suggests that the very dry climate has resulted in the recognizably different *M. auratus*. This population appears to have been isolated long enough to become specifically distinct, a conclusion that is supported by the cross-breeding experiments. Evolutionary factors of less influence may be causing the differences in karyotypes of *M. brandti* without producing reproductive isolation or obvious differences in phenotype.

NATURAL HISTORY

Published observations of *M. brandti* under natural conditions are scanty, the most complete being that of Argiropulo (1939) who studied this species in the Caucasus. Because his paper is written in Russian, a brief summary is included here, supplemented with field notes taken by Mr. Anat when he was trapping hamsters for us in Turkey. Both sources agree that the habitat of *M. brandti* consists of dry, rocky steppe country sometimes bordering cultivated fields. These hamsters do not inhabit wooded or bushy areas, and appear to avoid areas of high humidity and dampness. In the Caucasus they are found at altitudes as high as 2800 meters. Although they may be seen at dawn and dusk, they are mainly nocturnal and feed principally at night. In the wild, they are relatively fearless, for Argiropulo observed that they were apt to stand on their hind legs facing an intruder in the agonistic posture so often seen in the Syrian hamster.

In order to observe these animals under as natural conditions as possible, a compound measuring 160 × 280 centimeters (cm) and filled with clay soil to an average of 30 cm was set up in our laboratory. One part of the area was made higher than the remainder by the addition of rocks up to three kilograms in weight, and part of the flatter surface was planted with ground pine. A sunken dish served as a water supply and the bare soil was moistened periodically. During the month of July, two male and three female five-week-old *M. brandti* were released simultaneously into the compound. Within a few hours there were numerous holes in the soil and all of the animals were underground. For the next four months, no animal was ever seen in the broad daylight, though they were seen above ground when light was failing in the evening or under dim artificial illumination at night.

During the period of observation, the animals were given Purina laboratory chow (Ralston Purina Co., St. Louis, Mo.) as food, which was thrown at random on the ground. Most of the food which was not eaten was stored underground during the night. Argiropulo noted that *M. brandti* stores both grain and grasses in its burrows. M. R. Murphy (personal communication) reports that *Mesocricetus auratus* obtains grain by standing on its hind legs, grasping the stalk with its front feet or pushing it down, and cutting the stalk with its incisors. The animal then eats the fallen grain or puts it in its cheek pouches. Numerous stalks of tall grasses with ripened ears were pushed into the soil of the compound to simulate growing grain and the animals were observed in the evening under dim illumination. In spite of the fact that these hamsters were the sixth generation of animals raised in the laboratory, with no exposure to any growing grain, they cut down the stalk and consumed the kernels as described above.

After the five hamsters had been in the compound for 130 days, they were removed using box traps, and a diagram of their tunnel system was constructed by squirting silicone foam (Froth Pak, Insta-foam Products Inc., Addison, Ill.) down the various holes and permitting it to harden. Once hardened, the earth was scraped away and a positive cast of the underground galleries was obtained. Although these casts show several points of interest, it must be borne in mind that the hamsters were limited in the depth of their digging by the floor of the room.

At the time that the casts of the burrows were made, we were unaware of the work of Argiropulo (1939) with detailed descriptions of burrows which he excavated in the Caucasus. However, within the limitations imposed by the artificiality of the compound, the two series of burrows were remarkably similar. Both Argiropulo and Anat note that the main entrance of the burrow, when on a flat surface, is an almost vertical shaft extending a meter or more in depth. The vertical shaft usually curves quite abruptly to a horizontal plane, and the galleries and rooms branch from this shaft. Mr. Anat indicates that the hamster burrows can always be distinguished from those of *Microtus* or *Citellus*, which may inhabit the same area, because the burrows of the latter two enter the ground at a slant. When a hamster burrow was made in a bank, Argiropulo found that it was nearly horizontal. This type of tunnel was usually abandoned in a few days after other tunnels had been dug and the space filled in

with dirt and feces. Both in the artificial situation and in the natural state there were several underground chambers. One or more of these chambers were used for storage of food. Another chamber was a nesting area which in the natural state was filled with dried grass. In the artificial compound, the nesting material was ground pine and shreds of a cardboard box that had been placed in the area as a surface shelter. Argiropulo found that one chamber was used exclusively as a latrine, but no such chamber was found in the artificial compound.

To observe the method of digging employed by the hamster, a narrow, rectangular, clear Plexiglas box measuring $62 \times 31 \times 3.5$ cm (inside dimensions) was constructed. The box was placed on edge with its long side down and filled with earth to a depth of 17 cm. A hamster placed on top of the earth was squeezed so that both of its sides touched the sides of the box. The animal was capable of moving forward or backward, or of turning around, but it could only rest comfortably with its body parallel to the long axis of the box.

After several minutes of exploration, the hamster always commenced digging in the earth. The rapidly moving front feet were used to displace the earth, with motions like a dog burying a bone. The loose dirt accumulated under the chest and abdomen. To move this dirt, the hind feet were thrust backward together, while the front feet were braced. During this maneuver, the hamster arched its back and lifted its head. If the animal was in a tunnel, the head-lifting served to tamp the earth on the roof of the tunnel. As the tunnel or the surface excavation became longer, the earth at the head of the excavation was moved to the tail by a series of parallel kicks of the hind feet accompanied by back arching and head lifting, as described above. After each set of kicks, the hamster moved backward about one-half the length of its body and resumed moving the earth. Use of the mouth and cheek pouches for moving dirt was not observed, though the animals often took small quantities of earth in their mouth as if to taste it.

The rapidity with which hamsters can move earth and dig tunnels marks these rodents as truly fossorial, and indicates that hamsters kept in laboratory cages are denied a significant part of their normal behavioral pattern. The lifting of the head to tamp the roof of the tunnel apparently has functional significance, for Argiropulo observed that the inside of the tunnels which he excavated were very smooth.

LABORATORY CARE AND REPRODUCTION

Turkish hamsters in this colony are now kept in individual 17 × 17 × 24 cm floored cages and given ample shavings for bedding. During breeding 23 × 23 × 38 cm cages are used. The hamsters do not thrive in wire bottomed cages. The animals are given water and Purina laboratory rat chow *ad lib.* with a slice of raw apple and 30 g rolled oats weekly.

In 1968–1969 the colony was greatly reduced due to "wet tail" diarrhea and osteomalacia. The diarrhea was partially controlled by adding 0.05 per cent tetracycline hydrochloride (Polyotic, Cyanamid) to the drinking water for a period of not longer than two weeks. Various diets, one consisting wholly of Purina mouse breeder chow, have been experimentally tested, but the diet outlined above has been most satisfactory. The cause of osteomalacia has not been determined, but since it no longer occurs in the colony, it probably was due to an insufficiency in the diet exacerbated by an intestinal infection which, in its most virulent form, resulted in "wet tail" and death.

Although it rarely occurs in *M. auratus*, several *M. brandti* suffered from malocclusion, so that the upper and lower incisors grew unchecked by wear. The unrestrained growth was remarkably rapid. In a three-month-old hamster the upper incisors had grown slightly more than a full circle with one incisor penetrating and exiting from the roof of the mouth. The lower incisors of a one-year-old hamster with malocclusion were trimmed periodically and the excess tooth material was measured. Growth averaged 1 cm per month compared to growth of approximately 0.4 cm per month reported by Sarnat and Hook (1941) in the much larger thirteen-lined ground squirrel (*Citellus tridecemlineatus*).

Pairs of hamsters from five weeks to two years of age were exposed to each other for breeding in every month of the year. The youngest female to produce a litter was 50 days old when she gave birth, and animals seven to eight weeks of age reproduce successfully though they have not yet attained full growth. Hamsters reach their peak of fecundity at about one year of age, and most of our breeding is carried out with animals of this age. The tests of one-year-old males are large during the breeding season and histological examination shows active spermatogenesis. Females of this age almost invariably have normal estrous cycles. In the second year, the female estrous cycles are less regular during the breeding season

though active spermatogenesis usually occurs in the males. Breeding is notably less successful in these animals. We have not attempted to breed three-year-old hamsters.

In our laboratory (Boston, Mass.), animals exposed to natural day length usually were not in breeding condition between the months of November and March. During this period the females which were examined were apt to have anestrous vaginal smears with a preponderance of non-nucleated squamous cells. The testes of some males were atrophic with no histological evidence of spermatogenesis, and no stored sperm in the epididymides. Other animals of both sexes had all the anatomical indications of full breeding condition. The testes were the same size as those of summer animals and histological examination revealed spermatogenesis, while biopsy of the epididymides showed motile sperm. Vaginal smears indicated normal estrous cycles.

In 1971, pairs of hamsters were exposed to each other from January to September. As was expected, successful breeding was low for the first three months of the year, improved in the next two months and then declined. Thus, from January 20 to April 3 there were 11 litters out of 33 exposures. Successful matings peaked in May, with seven litters born out of 13 exposures. From June 1 to September 3, there were only 11 litters born in 34 exposures.

From 1966 to 1971 various changes in daily illumination and diet were carried out in order to discover the optimum conditions for breeding this species in the laboratory. During the first two years after their arrival, the animals were maintained on 10 hours of illumination in each 24 hour period. Breeding success was high during the first summer (1966) with a total of 109 young in 16 litters being produced by 23 pairings from the wild-caught group of six males and seven females. During the next summer there was a notable decline in successful matings. Of a total of 79 pairings with 42 males and 45 females, only 111 young in 15 litters were produced. In the case of unsuccessful pairings, the female always appeared to be the unwilling one of the pair.

In the difficult years of 1968 and 1969 the colony barely maintained a steady population, but by 1970 a successful diet had been developed, the daily lighting had been standardized to the illumination of this latitude, and attempted breedings were usually limited to the spring and summer months. Under this regime, breeding success improved, with 17 litters in 34 matings in 1974.

Hoffman and Reiter (1965) and Elliott et al. (1972) have reported that the reproductive cycle of the male Syrian hamster is responsive to photoperiod. A controlled experiment to test this responsiveness in the Turkish hamster has not been carried out, but the birth of litters in January and February, with the day length near the minimum, shows that the photoperiodic effect is not absolute. Data presented below indicate that hibernation is involved in a much larger segment of the yearly life of the Turkish hamster than is the case in the Syrian species. Turkish hamsters which are exposed to a constant temperature of 22°C in the laboratory during the winter months are living in an environment which they would never encounter for long periods in the natural state. It is not surprising that photoperiod alone does not control the seasonal sexual cycle under these circumstances.

The breeding behavior of the Syrian hamster has been described by Murphy and Schneider (1970) and the behavior of the Turkish hamster is similar. When the animals were paired in the afternoon, there was usually some preliminary exploration, but not much activity occurred until nightfall. In some cases, however, an immediate antipathy developed and violent fighting occurred at once.

After the first half hour of exposure, fighting was not as frequent, but it could occur at any time. If the animals were kept together for more than four days the chances of fighting increased, perhaps because the female was pregnant. Fighting was always violent, with the female biting the male near the head region and then clawing him with both front and rear feet. The male, in spite of the punishment he received, often followed the female and attempted to copulate, only to be attacked again. If the male retreated, the female often pursued him and bit him on the flanks and hind quarters. Attempts to reduce the damage to the male by providing various shelters were unsuccessful because of the male's persistence in pursuing the female. Often the punishment received by the male was fatal. At autopsy the cuts and bruises did not seem sufficiently severe to cause death and it is possible that exhaustion was a contributing cause.

The estrous cycle of the Turkish hamster is similar to that described by Kent (1968) for the golden hamster. The cycle is of four days duration and estrus is characterized by the appearance of large numbers of nucleated epithelial cells in the vaginal smear.

Gestation is 15 days in length and the litter size has varied from one to 13 with the average being six (N young = 1021, N litters = 177).

No female has produced more than three litters during one breeding season and Argiropulo (1939) reports that two litters a year is maximum for wild animals in the Caucasus. The female becomes extremely apprehensive before the birth of her litter, and partial darkness and ample bedding are a necessity. Even if left undisturbed she may kill and eat the young, and if she is handled during parturition the destruction of the litter is inevitable. Perhaps a littering cage which approximated the fossorial existence in the wild would reduce this nervousness, but this has not been tested.

Hamsters are born blind and naked, but they quickly grow a protective coat. By the twelfth to thirteenth day the eyes open and the young eat rolled oats, ground laboratory chow and drink from the water bottle. The young are weaned by the mother before the twentieth day, and we routinely separate the young from the mother at four weeks of age.

The young live together amicably until about the seventh week, when fighting starts to occur. Usually one animal is the aggressor, but if it is removed from the litter, another soon takes up the role. The attacked animal is bitten violently, resulting in large wounds from tears in the tender skin, and these are often fatal. Presumably, under natural conditions this aggressive behavior causes dispersion of the litter with little harm to its members, but in the laboratory it is a serious problem. Although we have used several types of shelters, we have not been able to keep Turkish hamsters in collective cages and must separate and maintain them in single cages at about six weeks of age. Obviously this is a serious disadvantage for maintaining a large colony.

The young hamsters grow rapidly, and healthy litters average 91 g in weight with a range of 50 to 141 g ($N = 411$) at six to seven weeks of age. Animals born after June do not attain sexual maturity until the following spring.

AGING

Turkish hamsters in captivity tend to become obese after the first year of life and sometimes weigh over 200 g, with our heaviest recorded animal attaining 285 g. It is unlikely that hamsters in the wild, with limited food supply and an active life, would ever reach this weight.

The median life-span of 43 animals which were bred and kept in the laboratory at a room temperature of $22 \pm 3°C$ was 670 days with a range of 231 to 1399 days. After about two years of age, the

pelage usually loses its glossy smoothness and the animals present a scruffy appearance. The effect of hibernation on aging in this or any other species of mammal is unknown and an experiment is in progress to determine if these hamsters age less rapidly during hibernation.

HIBERNATION

During the past ten years, quite complete records of the colony of *M. brandti* have been maintained, so that some information can be gleaned concerning the putative factors which control hibernation. Previous observations on *M. auratus* in this laboratory (Lyman, 1954; Lyman, unpublished observations) provide comparison between the two species.

In those studies, all hamsters were moved to a cold room kept at $5 \pm 2°C$ and lighted 8 to 10 hours a day. The animals were housed in individual cages with ample shavings and food and water *ad lib.* Hibernation was monitored by dusting the backs of hibernating Syrian hamsters with shavings. If the shavings were still in place at the next observation, hibernation was assumed to be continuous. This technique is common among students of hibernation (Mrosovsky, 1971) but is not always accurate. Because hamsters often burrow in their bedding before hibernation, shavings occasionally become lodged on the back and the hamster may be erroneously scored as being in continuous hibernation. Following the technique of Johnson (1931), extraneous material (rolled oats) was placed on the backs of the hibernating Turkish hamsters. Arousal from hibernation invariably displaced this material. The result of this difference in technique is to make the Syrian hamsters appear to be "better" hibernators than they actually are.

The timing and period of cold exposure was not the same for *M. auratus* and *M. brandti.* The former were moved to the cold at various times of year and remained there until they hibernated or died. In contrast, because it was necessary to enlarge the *M. brandti* colony, most of these animals were exposed to cold in the autumn and removed to the warm room for breeding in the spring. The fact that the *M. auratus* were moved to the cold in all seasons of the year should have no effect on the comparisons given below. Smit-vis and Smit (1963) have theorized that there is a seasonal preparation in this species which results in a greater tendency for

hibernation in February. The evidence is not persuasive, however, for it is based on 26 animals, two of which are excluded from the basic computations. The paper relates the month in which the animals were exposed to cold to the lapse of time before hibernation occurred, but there are no data for April through July or for September and October, and there is data for only one animal in August and two in March. From our records of over 2800 Syrian hamsters, placed in the cold in every month of the year, we adduce no convincing evidence that the tendency to hibernate is seasonal in this species.

In studies such as this, an as yet unresolved problem concerns the criteria which should be used to distinguish "good" from "poor" hibernators. There are at least five interdependent factors which can be considered in such a comparison. These are: 1) the number of animals in a group which hibernate during the period of exposure to cold, 2) the span of time between cold exposure and hibernation, 3) the length of the hibernating season, 4) the amount of time spent in hibernation compared to the amount of time in the cold, and 5) the length of the period during which an animal remains in continuous hibernation. Concerning the fifth factor, Pengelley and Fisher (1961) have shown that the lengths of the periods or bouts of hibernation are quite predictable with individual *Citellus lateralis*, but these lengths may vary greatly in a group. We find that the same situation obtains in *Mesocricetus* so that the maximum time of uninterrupted hibernation is more definitive than an average of the lengths of the bouts of hibernation. Until more is known about the subtle physiological nuances which determine whether an animal does or does not hibernate, it is not practical to attempt to assign meaningful values to the five factors listed above, nor to make statistical comparisons. Therefore, in the following studies as many factors as possible are considered but no attempt is made to weight their importance.

In a group of 373 Syrian hamsters exposed to the cold, 68 per cent or 252 hibernated and 121 animals died before ever entering the hibernating state. The shortest period before hibernation occurred was three days of cold exposure and the longest was 218 days (Lyman, 1954). Once hibernation occurred, the period during which *M. auratus* hibernated lasted about three months. An accurate figure on the percentage of time spent in hibernation cannot be obtained because many of the animals were used in acute experiments and the best hibernators were usually chosen. The longest

recorded bout of hibernation was 21 days and the usual period of hibernation was a week or less (Lyman, 1954).

The hamsters from which these data were collected were originally obtained from commercial dealers and hence must be descendants of the trio which were the foundation stock of the laboratory hamsters used today (Adler, 1948). Twelve *M. auratus*, which were the first generation of animals obtained in the field near Aleppo by Dr. M. Murphy, were exposed to the cold in the autumn of 1971 under the conditions described above. Although the sample is small, there was no detectable difference in the tendency of this group of animals to hibernate when compared to laboratory animals. Thus, forty years of domestic breeding with no selection pressure for hibernation has not changed the pattern of hibernation in *M. auratus*.

These "native" Syrian hamsters provide some information concerning the percentage of time spent in hibernation. The group was moved to the cold on November 15, 1971 and taken from the cold on May 26, 1972. No animal hibernated before January and hibernation occurred only 11.3 per cent of the total time. The best months for hibernation were January through April, during which time the animals were in hibernation 13.7 per cent of the time.

Between the years 1971 and 1975, a group of 318 *M. brandti* were exposed to cold for periods of 145 to 172 days. Two hundred ninety-three or 92 per cent hibernated at some time during this period. Eight animals died without hibernating and the remaining 17 did not hibernate at all. Thirty-one animals entered hibernation within 24 hours after exposure to cold. Once hibernation started, the period during which this species hibernated lasted about five months, but for some animals the hibernating season was as long as 10 months. In the entire group, 36 per cent of the time in the cold between November 15 and April 15 was spent in hibernation. The longest period of uninterrupted hibernation was 28 days, with the average bout of approximately the same duration as *M. auratus*. Thus *M. brandti* is a "better" hibernator than *M. auratus* in all categories except the average length of the bout of hibernation.

The records of over 400 *M. brandti* which have been exposed to cold reveal no obvious factors which control or influence hibernation in this species. However, they do give a clearer picture of the pattern of hibernation and its variability, and obviate the need for further research in some aspects of the problem.

As reported for *M. auratus* (Lyman, 1948), *M. brandti* does not undergo the period of autumnal fattening and lethargy which is so typical of the Marmotini that hibernate. Like *M. auratus, M. brandti* almost invariably lose weight during the first two or three weeks of exposure to cold, with the heavier animals losing the greater amount. Some animals, especially the young of the year, are apt to regain and exceed the original weight if kept in the cold for several months. The amount of hibernation which occurs during this time is not correlated with the change in body weight.

Examples from the spring and summer months demonstrate that this species will hibernate at any time of the year. Certainly, if compared to Marmotini such as *Citellus lateralis* or *C. tridecemlineatus*, any seasonal change in the tendency to hibernate is very poorly defined. These citellids, if experimentally naive, rarely hibernate when exposed to cold during the spring and summer months and almost invariably hibernate in the autumn. In contrast, of 66 *M. brandti* which were in the cold in June, 75 per cent hibernated at some time during the period and, in July, 77 per cent of 53 cold-exposed animals hibernated.

The majority of our animals were placed in the hibernaculum between October 1 and January 2. In a sample of 257 animals, no particular one of the four months was favored for onset of hibernation or for the number of days spent in the hibernating state. Whether exposure to cold was begun in early October or in January, hibernation became much less frequent by the beginning of April and, when removed from the cold room in May, most of the animals had ceased hibernating.

No organized experiment to test the effect of photoperiod has been carried out, but it is clear that the timing of the onset of hibernation does not depend exclusively on this factor, since hamsters hibernated in June when the daily illumination was close to its peak.

Although 9.7 per cent of a sample of 318 animals hibernated within 24 hours after being exposed to cold, these animals did not necessarily hibernate for a greater number of days than animals which started hibernation at a later date. Age does not affect the ability to hibernate, for a comparison between animals ranging from 3.5 to 36 months of age revealed no differences in the onset or pattern of hibernation.

In spite of efforts to standardize conditions, the frequency and pattern of hibernation changed from year to year in the colony as

a whole and with individual animals. There is no simple explanation for the fact that individuals failed to hibernate with six months of cold exposure one year, and hibernated under the same conditions the following year. Nor can the observation that the colony exposed to cold hibernated only 16 per cent of the time in 1970 and 39 per cent in 1971 be readily explained. Conditions in the cold room are maintained as identically as possible from year to year, but changes such as shifts in caretaking personnel are inevitable. Even differences in handling the animals during cleaning of the cages might influence the onset of hibernation.

It was observed that the first shipment of *M. brandti* hibernated 67 per cent of the first sojourn in the cold and only 42 per cent in the second. This suggested that environmental factors might play an important role in the control of hibernation. The ability of animals to store food had already been shown to have an effect on hibernation in *M. auratus* (Lyman, 1954) and this factor was included in the experimental design.

M. brandti between five weeks and six months of age were placed in the following experimental conditions. As often as possible, sexes and litter mates were matched. On July 8 five animals were placed in the "natural" compound described above. For all other groups, each individual was put in a separate cage (23 × 23 × 38 cm) and given ample shavings for bedding, and water *ad lib.* A control group of 13 animals was given Purina rat chow pellets *ad lib.*, which they were able to store in a corner of the cage, while another group of six was given ground chow in unspillable food cups which prevented these animals from storing food. Twelve other cages were fitted with exercise wheels, and the number of revolutions for each wheel was monitored by an event recorder (model A620X, Esterline Angus Instrument Co., Indianapolis, Ind.). The animals in six of these cages were given rat chow pellets *ad lib.* while the others were fed from unspillable food cups. All animals received 14 hours of light daily at the start of the experiment, and this was reduced by one hour approximately every 16 days. On November 12 all animals were moved to smaller individual cages (17 × 17 × 24 cm) with shavings, water and rat chow pellets *ad lib.*, and on November 15 all were moved in these cages to the cold room, where the daily illumination was 9 hours. Thus, after the preparation period, all animals were exposed to the same conditions. Records of hibernation were kept for the following 137 days.

As has been reported for many other species, the use of the activity wheel varied greatly from animal to animal. The nocturnal habits of *M. brandti* were verified, for virtually no activity was recorded during the daylight hours. There was no correlation between the tendency of an animal to run in the wheel and its subsequent hibernation. All of the hamsters hibernated at some time during their exposure to cold, but no one group showed a tendency to enter hibernation earlier or to have longer bouts of hibernation. The percentage of time spent in hibernation was as follows: "natural" enclosure, 56 per cent; activity wheel, food hoarding, 43 per cent; no wheel, food hoarding, 37 per cent; wheel, no hoarding, 34 per cent; no wheel, no hoarding, 25 per cent. These results suggest that the conditions prior to cold exposure may have an influence on the subsequent amount of hibernation and that "natural" conditions increase the tendency to hibernate. However, none of the factors tested are crucial to the onset of hibernation.

Experiments such as these are easily carried out with *M. brandti*. Because this animal hibernates readily and can be bred in the laboratory, it offers a unique opportunity to study the effects of various factors using matched pairs of known age and lineage.

ACKNOWLEDGMENTS

This research was supported by grants from the National Institutes of Health and contracts with U.S. Air Force.

In this ten year study many people contributed their help. We are particularly grateful to Jane L. Bihldorff, Michael F. Carr, Helen Cheever, and Delphi M. Toth. We owe great thanks to Dr. N. Kalabukhov of the Far East Scientific Center of the Academy of Sciences, Vladivostok, USSR, who has been most helpful in giving advice and references concerning the species of *Mesocricetus* in the USSR. We are indebted to Barbara Lawrence for her critical review of the manuscript, but any errors or ambiguities are uniquely our own.

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